Arbuscular Mycorrhizal Fungi

Occurrence in Sweden and Interaction with a Plant Pathogenic Fungus in Barley

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Cover photos of a barley field at the SLU research station at Offer, a barley root and a hyphae of *Glomus intraradices*, a barley plant in Switzerland with spot blotch and a spore of *Gigaspora margarita*. All photos are taken by Johanna Sjöberg (except the spot blotch which is taken by Sara Elfstrand).

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To my parents

Marianne & Nils-Gunnar Sjöberg

Med goda idéer är det som med svamp;
där man hittar en finns det oftast flera
Okänd

Om du tänker för länge på nästa steg,
kommer du tillbringa livet på ett ben
Kinesiskt ordspråk

Abstract

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The potential disease suppressiveness of arbuscular mycorrhizal (AM) fungi of various origins on *Bipolaris sorokiniana* in barley has been investigated. Firstly, a survey considering the occurrence of AM fungi in arable fields in Sweden were conducted with the aim to exploit site specific genetic resources in relation to disease suppressiveness. Arbuscular mycorrhizal fungi were present at all 45 sampling sites surveyed all over Sweden at densities ranging from 3 up to 44 spores per gram air dried soil. The highest spore density was found in a semi-natural grassland and the lowest were found in a cereal monoculture. The AM fungi were then multiplied in trap cultures in the greenhouse with the aim to use these for studying potential disease suppressiveness. Thus, the effects of the AM fungi trap cultures on the transmission of seed-borne *B. sorokiniana* in barley were investigated, using the trap culture inocula, but also including inocula consisting on spore mixtures. The arbuscular mycorrhizal fungi were able to suppress the transmission of *B. sorokiniana* in aerial parts of barley plants. The degree of suppression varied with the origin of the AM fungal trap cultures. The trap culture inoculum with the highest suppression of the *B. sorokiniana* transmission originated from an organically managed barley field with undersown ley. The two spore-inocula with the best suppression of the pathogen originated from fields with winter wheat and spring barley, respectively.

Eventually, an *in vitro* method was developed for studying the effect of AM fungal colonisation of roots on the development of foliar diseases and the reaction of the actual host plant of the disease causing organism. Using the developed method, it was indicated that AM fungal colonisation of barley plant suppressed the development of leaf necroses due to *B. sorokiniana*. Further *in vitro* studies on the interaction between *B. sorokiniana* and arbuscular mycorrhizal fungi showed that *B. sorokiniana* decrease the germination of the AM fungal spores. In conclusion, AM fungi suppress the development of *B. sorokiniana* in barley. My data suggest that for biocontrol of *B. sorokiniana* AM fungi should be considered.

Key words: Biocontrol, *Bipolaris sorokiniana*, Glomeromycota, Common root rot, Spot blotch

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Svensk sammanfattning

Bipolaris är en växtsjukdomsframkallande svamp som under svenska förhållanden i första hand angriper korn. Svampen sprids främst via utsäde, men det kan även finnas smitta i jord eller luft. Svenska försök har visat skördeförluster på närmare ett halvt ton per hektar. Syftet med mitt doktorandprojekt var att ta reda på om arbuskulär mykorrhizasvamp kan minska angrepp av bipolaris i korn. Arbuskulär mykorrhizasvamp är en svamp som enbart kan leva genom att samverka med växtrötter. Svampen får energi genom växtens fotosyntes och i gengäld hjälper svampen växten att ta upp näring. Svampen har fått sitt namn genom en speciell struktur som kallas ”arbuskler”. Arbusklerna är förgrenade hyfer i rötternas celler där näringsutbytet sker. Till att börja med inventerades arbuskulär mykorrhizasvamp i svensk åker- och ängsmark, därefter studerades effekten av arbuskulär mykorrhizasvamp från olika fält på utsädesburen bipolaris och sist gjordes en studie för att ta reda på om de båda svamparna har någon direkt inverkar på varandra. Arbuskulär mykorrhizasvamp fanns i samtliga 45 fält där jordprov togs, från Skåne i söder till Norrbotten i norr. Det visar att arbuskulär mykorrhiza har en stor utbredning i svensk jordbruksmark. Växthusstudier visade att arbuskulär mykorrhizasvamp hämmar bipolaris utveckling från utsädessmittan till blad och strån. Mykorrhizasvampar från olika fält var olika effektiv beträffande hämning av bipolaris. Mykorrhizasvampen hämmade bipolaris, trots att det var låg kolonisering av mykorrhizasvampen i rötterna. Det kan tyda på att bipolaris i sin tur hämmar mykorrhizasvampen. I laboratoriestudier visade det sig att bipolaris hämmar groning av den arbuskulär mykorrhizasvampens sporer. Extrakt från mykorrhizasvampen hade däremot ingen inverkan på groning av bipolariskonidier. Dessutom utvecklades en metod för att under sterila former kunna studera effekten av mykorrhizakolonisering av kornrötter på olika sjukdomar på bladen. Med denna metod kunde det påvisas att kolonisering av arbuskulär mykorrhizasvamp hämmade utvecklingen av bipolarisfläckar på bladen. För biologisk bekämpning av bipolaris i korn är det förmodligen möjligt att påverka brukningsmetoderna för att främja groning och aktivitet av de mykorrhizasvampar som har störst förmåga att hämma patogenen.

Contents

Appendix

Paper I-III

The thesis is based on the following papers;

I. Sjöberg J., Persson P., Mårtensson A., Mattsson L., Adholeya A. & Alström S. 2004. Occurrence of Glomeromycota spores and some arbuscular mycorrhiza fungal species in arable fields in Sweden. *Acta Agriculturae Scandinavica, Section B, Soil and Plant Science 54*, 202-212.

II: Sjöberg J., Mårtensson A. & Persson P. Development of seed-borne *Bipolaris sorokiniana* in barley in the presence of field populations of arbuscular mycorrhizal fungi. European Journal of Plant Pathology (Accepted after minor revision).

III. Sjöberg J. The plant pathogenic fungus *Bipolaris sorokiniana* inhibits arbuscular mycorrhizal fungi which in turn suppress disease development in barley. Mycorrhiza (Submitted).

Paper I is reprinted by permission of the publisher

Objectives

In this thesis I have studied the occurrence of arbuscular mycorrhizal (AM) fungi in arable fields in Sweden, the influence of AM fungi from different origin on *Bipolaris sorokiniana* infested barley plants and the mechanisms involved in the interactions. The hypothesis was that the AM fungi can inhibit the transmission of *B. sorokiniana* in barley and that these characters differ with the origin of the AM fungi. A second hypothesis was that the AM fungi and *B. sorokiniana* affect the germination or hyphal growth of each other in the preinfectious stage in the soil. To test the hypotheses field and laboratory studies have been conducted at different scales; from the field level occurrence of AM fungi in a country to the micro scale of individual fungal hyphae growing on nutrient medium in the laboratory. A series of studies were conducted with the aims to:

- investigate the occurrence and diversity of arbuscular mycorrhizal fungi in arable fields in Sweden (Paper I),
- investigate the influence of AM fungi from different fields on the transmission of seed-borne *B. sorokiniana* in barley (Paper II),
- study the mechanisms involved in the interactions between *B. sorokiniana*, AM fungi and barley plants (Paper III).

Introduction

Plants are, by definition, the only higher organisms that can convert the energy of sunlight into stored, usable chemical energy. The farmers are a link through which this energy becomes food to domestic animals and humans. However, not only humans take advantages of this life necessity, but also fungi around the plant roots, among those both harmful- and beneficial organisms, influencing the quality and yield of the crop. The former includes the widespread plant pathogenic fungus *Bipolaris sorokiniana* that can cause disease in grasses including cereals but occasionally also other taxonomic groups (Wildermuth and MacNamara, 1987). *Bipolaris sorokiniana* is an important pathogen of barley in the cool climate of North-Western Europe (Jørgensen, 1974; Whittle, 1977; Kurppa, 1984). Only in Scandinavia barley (*Hordeum vulgare* L.) is cultivated on an area of nearly two million hectare (Statistics Sweden, 2004), mostly spring barley. There has been increasing demand for non-chemical methods of plant disease control, both from consumers and farmers. Extensive uses of pesticides pose a risk for pollution of the environment and the food, with sometimes well-known, sometimes poorly known consequences. The development of plant pathogen resistance to commonly used chemical compounds is another risk factor. An additional threat is that fungicides may reduce plant beneficial organisms. Beside the need of decreasing the use of synthetical chemicals, there is also a need for organic farmers to achieve tools for restricting the negative consequences of the pathogens.

A few studies have indicated the possibility of arbuscular mycorrhizal (AM) fungi to suppress *B. sorokiniana* in the roots (Dehn and Dehne, 1986; Thompson and Wildermuth, 1989). The use of AM fungi, either by adding them into the field or by favouring the already existing, could therefore be an interesting alternative or complement to restrict the pathogen.

Arbuscular Mycorrhizal Fungi

Taxonomy

The first report that root fungi may be beneficial to plants was observed on Indian pipe (Kamienski, 1881). Frank (1885) named the symbiosis between fungi and roots "Mykorrhizen", from the Greek meaning "fungus root". Amongst the mycorrhizal associations, the AM association is the most common one. Arbuscular mycorrhizal fungi belong to the fungal phylum Glomeromycota (Schüßler et al., 2001). The Glomeromycota is divided into four orders, eight families and ten genera. The genera which include most of the described species are *Acaulospora*, *Gigaspora*, *Glomus* and *Scutellospora* (Schüßler, 2005). The AM fungi obtain their energy through an obligate symbiosis with vascular plants; the AM, although non-vascular plants also are reported to form the AM (Russell and Bulman, 2005). The AM fungi are named by their formation of highly branched intracellular fungal structures or "arbuscules" which are the site of phosphate exchange between fungus and plant. Vesicles, which contain lipids and are carbon storage structures, are formed commonly in most genera of Glomeromycota, although this will depend on environmental conditions (Smith and Read, 1997). Gianinazzi-Pearson (1996) pointed out that these obligatory biotrophs, the AM fungi, have a very broad host range, which makes them definitely different from the biotrophic fungal plant pathogens as well as other root symbionts.

Fossil records suggest that the AM symbiosis dates back to the Ordovician age, 460 million years ago (Redecker et al., 2000). These fossils indicate that Glomeromycota-like fungi may have played a critical role in facilitating the colonisation of land by plants. As AM fungi are obligate symbionts, they are not yet successfully cultured in the absence of plant root. The symbiosis is normally mutualistic and based on bi-directional nutrient transfer between the symbionts. However, the mycorrhizal association may vary along a symbiotic continuum from strong mutualism to antagonism (Carling and Brown, 1980; Modjo and Hendrix, 1986; Howeler et al., 1987; Johnson et al., 1997). More than 150 species are described within the phylum Glomeromycota on the basis of their spore development and morphology, although recent molecular analyses indicate that the definite number of AM taxa may be much higher (Daniell et al., 2001; Vandenkoornhuyse, et al., 2002). However, the biological knowledge is lacking for some of the described species and others are synonyms (Walker and Trappe, 1993; Walker and Vestberg, 1998). All members of the AM fungi are asexual and the vegetative mycelium and intraradical structures are aseptate and multinucleate. Most spores are between 50 and 500 μm in diameter depending on the species.

Another type of mycorrhizal association is the ectomycorrhiza, in which the fungal hyphae form a mantle consisting of densely interwoven hyphae around the

root. From this mantle external hyphae grow into the surrounding soil. Hyphae also grow inside the root forming the Hartig net in the spaces between epidermal and cortex cells. In addition, to the arbuscular- and ectomycorrhiza, the mycorrhizal associations can be classified into four other types based on the type of fungus involved and the range of resulting structures produced by the root-fungus combination (Table 1; Harley, 1959; Harley and Smith, 1983; Smith and Read, 1997; Read, 1998).

Table 1. The diagnostic structural features of the six recognised types of mycorrhiza (after Read, 2002)

Mycorrhiza		Fungi	Plant	Defining structures
Category	Type			
Sheathing[a]	Arbutoid	Ascomycetes Basidiomycetes	Arctostáphylos Arbutus Pýrola	Hartig net and intracellular penetration[c]
	Ecto	Ascomycetes Basidiomycetes	Coniferous and broadleaved forest trees	Hartig net, mantle, external mycelial network
	Monotropoid	Basidiomycetes (selected ecto fungi)	Monotropáceae	Fungal pegs
Endo[b]	Arbuscular	Glomeromycetes	Most families	Arbuscules Hyphal coils
	Ericoid	Ascomycetes Hymenoscýphus Oidiodendron	Ericáceae Epacridáceae Empetráceae	Hyphal complexes in hair roots
	Orchid	Basidiomycetes Rhizoctonia (some ecto fungi)	Orchidáceae	Peletons

[a]the root surface is sheathed in a fungal mantle, [b] lacking a mantle but in which hyphae proliferate internally, [c] also seen in the subtype "ectendo" .

Occurrence

Members of more then 80% of extant vascular plant families are capable of forming the AM. In addition, AM fungi are widely distributed on the earth. They are reported from all continents; Africa (Redhead, 1977), Antarctica (Cabello, et al., 1994), Asia (Al-Garni and Daft, 1990; Ganesan et al., 1991), Oceanien (Hall, 1977), North America (Walker et al., 1982; Dalpé and Aiken, 1998), South America (Siqueira et al., 1989; Aguilera et al., 1998; Vestberg, 1999; Caproni et al., 2003) as well as Europe (Land and Schönbeck, 1991; Blaszkowski, 1993; Vestberg, 1995; Jansa et al., 2002). Arbuscular mycorrhizal fungi colonisation of plants have been observed over a wide range of soil pH (Read et al., 1976), soil phosphate levels (Crush, 1975; Hayman et al., 1976; Jeffries et al., 1988) and salinity (Gerdemann, 1968). There are, however, marked differences considering distribution and abundance among species and strains of AM fungi in response to soil properties.

Colonisation

There are three important components of the mycorrhizal root system (Figure 1); the root itself, the intraradical mycelium (the fungi within the root) and the extraradical mycelium (the fungi within the soil). Colonisation of roots by AM fungi can arise from spores, infected root fragments and/or hyphae . The spores are formed on the extraradical hyphae, but some species also may form spores inside the roots. Soluble exudates or extracts from the roots of host species stimulate the

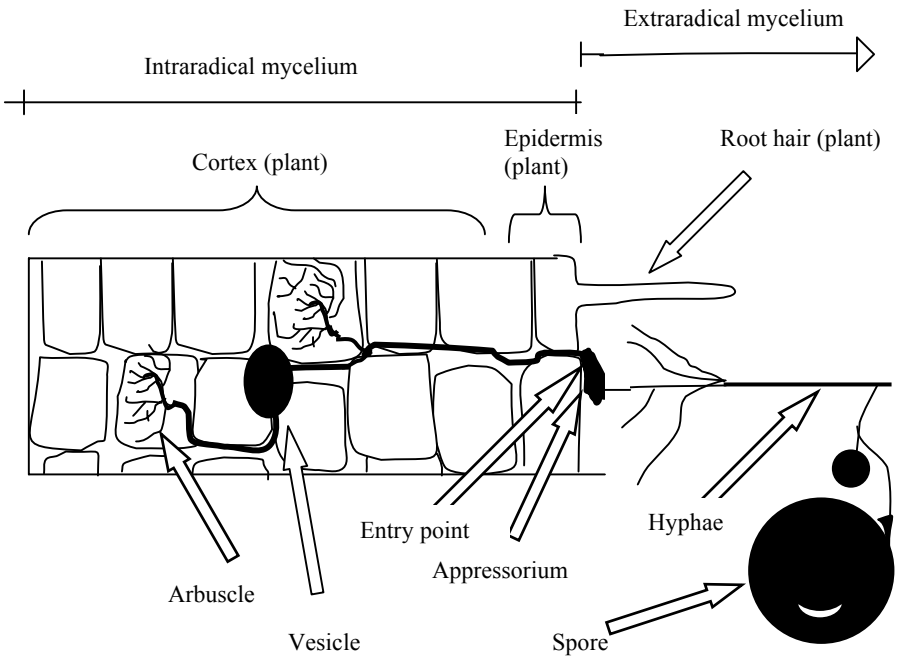

Figure 1. Simplified section of mycorrhizal root and external mycelium of arbuscular mycorrhizal fungi as seen on the microscope. The arrows point out the fungal structures.

growth and branching of mycelium growing from spores (Graham, 1982; Elias and Safir, 1987; Gianinazzi-Pearson et al., 1989), while the exudates from a non-host had no effect (Gianinazzi-Pearson et al., 1989). The main hypha approaches a root often gives rise to a fan-shaped complex of lateral branches, which is thinner and may be septate, and colonisation of the root usually occur from these hyphae (Mosse and Hepper, 1975; Giovannetti et al., 1993a,b). Hyphal contact with the root is followed by adhesion and formation of swollen appressoria preceding the penetration (Bécard and Fortin, 1988; Giovannetti et al., 1993b). There is evidence that the host plant recognise the AM fungi already at this stage, which is indicated by regular occurrence of slight wall thickening on the epidermal cell adjacent to the penetrating hyphae (Garriock et al., 1989). The thickenings do not contain either callose or lignin and do not prevent the penetration of fungal hyphae through the walls (Harrison and Dixon, 1994).

There are two types of mycorrhiza according to the structures of the intraradical mycelium; the Arum-type and the Paris-type (Gallaud, 1905). In the Arum-type the fungal symbiont spread in the root cortex via intercellular hyphae. Short side-branches penetrates the cortex cells and produce arbuscules. The Arum-type is commonly described in fast growing root systems of crop plants. In the Paris-type the hyphae develop intracellular coils and spread directly from cell to cell within the cortex. Arbuscules grow from these coils. Co-occurrence of Arum- and Paris-type morphologies of AM is found in cucumber and tomato (Kubota et al., 2005). Arbuscules are usually relatively short-lived, at least in the Arum-type mycorrhiza and the hyphae are comparable long-lived (Holley and Peterson, 1979; Smith and Dickson, 1991). The arbuscules progressively degenerate, whilst the plant cell remains alive, which is a difference compared to many plant pathogenic fungi which cause plant cell death. For rapidly growing crop species the formation of arbuscules may take 2-3 days and the whole arbuscular cycle approximately seven days (Bevege and Bowen, 1975; Brundrett et al., 1985).

The extraradical mycelium consists of two distinct types of hyphae, the runner hyphae and the absorbing hyphae (Friese and Allen, 1991). The runner hyphae are thicker and grow through the soil in search of roots. The hyphae that penetrate roots are initiated from runner hyphae. The absorbing hyphae also develop from the runner hyphae and form a network of thinner hyphae extending into the soil. These hyphae appear to be the component of the fungus that absorbs nutrient from the soil for transport to the host. Arbuscular mycorrhizal fungi can associate with multiple hosts, including different species (Hirrel and Gerdemann, 1979; Heap and Newman, 1980; Warner and Mosse, 1983; Read et al., 1985; Molina et al., 1992). Some mycorrhizal plants are thus probably interconnected by a common mycorrhizal network (Newman, 1988). This means, for example, that there is a movement of carbon from the root of one plant, through AM fungi, to roots of other plants (Francis and Read, 1984; Graves et al., 1997).

Benefits for the AM symbionts

As all mutualistic beneficial cooperations, both partners (fungi and plant) have advantages of the symbiosis. Carbon from the photosynthesis are used by the fungi and the plant make use of the extended soil volume. The AM fungi take up a significant fraction of all plant photosynthetically fixed carbon (Paul and Kucey, 1981). In a field study, between 3.9 and 6.2% of the fixed carbon are shown to be passed through the external mycelium of the AM fungal symbiont to the atmosphere (Johnson et al, 2002). The fungus acquires carbon as hexose within the root (Shachar-Hill et al., 1995; Solaiman and Saito, 1997), but it is stored primarily as triacylglycerol (Cox et al., 1975; Beilby and Kidby, 1980; Beilby, 1983; Jabaji-Hare, 1988; Gaspar et al., 1994), but also as glycogen (Bago et al., 2003). The net movement of storage lipid is from the intraradical mycelium to the extraradical mycelium, although there is also substantial recirculation throughout the fungus (Bago et al., 2002).

In return for the carbon, the mycorrhizal plant obtains nutrients such as, for example, inorganic phosphate via the AM fungal hyphae. The inorganic phosphate, as also other inorganic nutrients such as zinc, is relatively immobile in

the soil solution, which leads to the formation of zones depleted in inorganic phosphorus around the roots. This depletion zones effectively limit phosphor uptake in non-mycorrhizal plants. The symbiotic association with AM fungi allows the plant to access phosphorus beyond the depletion zone through the extraradical fungal hyphae, in addition to the root uptake (Pearson and Jakobsen, 1993). Arbuscular mycorrhizal fungi also contribute to the uptake by plant of micronutrients, such as zinc (Thompson, 1990) and the macronutrient nitrogen, both inorganic and possibly also organic (George et al. 1995; Hawkins et al., 2000; Hodge et al., 2001). In addition to the nutrient uptake activity, the extraradical mycelium also releases substances that cause the soil and its organic components to aggregate (Sutton and Shepard, 1976; Tisdall and Oades, 1979; Tisdall, 1991; Tisdall, 1994; Bearden and Petersen, 2000). Another impact of AM fungi on the plants, including agricultural crops are their ability to increase their tolerance to drought (Davies et al., 1993) and reduce damage caused by plant pathogens (Dehne, 1982; Borowicz, 2001; Whipps, 2004). Hormonal changes throughout the entire plant under the influence of the symbiosis have also been described (Allen et al., 1980; Allen et al., 1982). Under some circumstances AM fungi are able to decrease negative effects by heavy metals in plants (Davies et al., 2001; Tonin et al., 2001; Rivera-Becerril et al., 2002).

Agricultural impact on AM fungi

Most of the cultivated plant species are able of forming the AM. However, the plant families *Brassicaceae* and *Chenopodiaceae* include species that do not usually form mycorrhizal symbiosis, among them sugar beet and rape (Tester et al., 1987). Growing these crops subsequently does not lead to any multiplying of AM fungi, unless there are weeds that can act as hosts (Abbot and Robson, 1991; Jansa et al., 2002). Mycorrhizal inoculum density also declines when soils are kept fallow for extensive periods of time (Black and Tinker, 1979; Thompson, 1987). The quantity of AM fungi in soils also differs between host species (Thompson, 1991; Vivekanandan and Fixen, 1991). Even the preceeding crop in a crop rotation system affect the AM fungal spore densities in the field and thereby the yield of the following crop (Thompson, 1991; Karasawa et al., 2001). Oehl et al. (2003) found that increased land use intensity was correlated with a decrease in AM fungal species richness and with a preferential selection of species that colonised roots slowly but formed spores rapidly. To remember is also that the most dominant species of AM fungi may not be the most beneficial mutualists. Johnson et al. (1992) showed that crop monocultures selected for AM fungi that were inferior mutualists. Thus AM fungi may be involved in the yield decline often observed in continuous monocultures. It has also been indicated that AM fungi from fertilised soil exert a higher net carbon cost on their host than AM fungi from unfertilised soil (Johnson, 1993). There is not only a difference between crop species in the degree to which they form mycorrhiza, there is also a difference between cultivars of the same species. Cultivars of wheat (Azcon and Ocampo, 1981; Young et al., 1985; Manske, 1990) and corn (Toth et al., 1984) have been shown to vary in levels of colonisation by AM fungi. In barley, an existing degree of host specificity is also indicated by Boyetchko and Tewari (1995) comparing yield and AM fungal colonisation of several barley cultivars

inoculated with AM fungi. The degree to which cultivars are colonised by, and benefit from, mycorrhiza is a heritable trait selectable through plant breeding (Krishna et al., 1985; Kesava et al., 1990).

By returning crop residues to soil the farmer might stimulate an increased mycorrhizal infection and spore population, which is shown in tropical forage systems (Saif, 1986). Disturbances such as ploughing have shown to reduce the functioning of AM fungi (Kabir, et al., 1997; McGonigle and Miller, 1999). Furthermore, application of farmyard manure is shown to increase densities of AM fungal spores, although this depends on the soil types (Kruckelmann, 1975; Harinikumar and Bagyaraj, 1989). Several studies indicate that cumulative P fertilisation decrease the spore density under Northern European field conditions (Jensen and Jakobsen, 1980; Mårtensson and Carlgren, 1994; Kahiluoto et al., 2001). Furthermore, AM fungal colonisation are shown not to be affected by P addition when plants are deficient in N but, when N was sufficient, P addition suppress root colonisation (Sylvia and Neal, 1990). Thus, there are cultivation measures available for the farmer to regulate the AM fungi at the field site. An important measure, apart from the choice of cropping systems, and cultivation is in conventional agriculture the use of fungicides. Systemic fungicides applied at field application rate are shown to reduce the functioning of the AM fungi (Menge et al., 1979; Kling and Jakobsen, 1997).

Plant and AM fungal diversity

The growth of many plant species is enhanced when AM fungi are present (McGonigle, 1988). It has also been shown in field and greenhouse experiments that AM fungi promote plant diversity in European grasslands (Grime et al., 1987; Gange et al., 1990, Gange et al., 1993; van der Heijden et al., 1998a). However, AM fungi can also reduce diversity, as has been observed in American tall grass praries (Hartnett and Wilson, 1999). The mycorrhizal dependency (or symbiotic effectiveness) of a plant shows the extent to which a plant benefits from the presence of AM fungi compared to when it is absent (Gerdemann, 1975; Plenchette et al., 1983; Johnson et al., 1997; van der Heijden et al., 1998b). Van der Heijden (2002) proposed that the number and relative abundance of mycorrhizal dependent plant species in the species pool of a community can be used to predict how AM fungi affect communities. Furthermore, recovery of disturbed ecosystems may depend upon the reestablishment of mycorrhizal fungi (Reeves et al., 1979; Janos, 1980; Allen and Allen, 1980; Perry et al., 1989).

However, not only the plants are affected by the AM fungi community, also the AM fungi respond to the plant diversity, as shown by comparing AM fungi community between plots cultivated with different number of plant species (Burrows and Pfleger, 2002). Species compositions of AM fungal communities also change during succession of abandoned arable fields (Johnson et al., 1991). When natural ecosystems are converted to agroecosystems the diversity of AM fungal communities tends to decrease, while diversity decreases as the intensity of agricultural inputs increases (Siqueira et al., 1989; Schenck et al., 1989; Sieverding, 1990). Since the species composition of AM fungal communities are influenced by plant species (Dodd et al., 1990; Johnson et al., 1991) this could be

an evidence of specificity between plants and AM fungi. Klironomos (2003) found a variation in response of different plant species to both different AM fungi co-existing with the plant in the nature and to AM fungi with an other origin than the plants. Since isolates of AM fungi differ in their effect on plants, Johnson and Pfleger (1992) stressed that highly diverse community of AM fungi may be desirable to increase possible options for host-fungus combination. On the contrary, less diverse AM fungal communities may be superior if the few fungal species that are present are good mutualists (Sieverding, 1990).

Bipolaris sorokiniana

Taxonomy

Bipolaris sorokiniana (Sacc. in Sorok.) Shoem. is a widespread fungus which can cause disease in barley, wheat and rice but also other grasses and infrequently other taxonomic groups (Wildermuth and MacNamara, 1987). An earlier name for the fungus was *Helminthosporium sativum* (Pamm. King and Blake), but the genus *Helminthosporium* has now been divided into *Drechslera* and *Bipolaris* (Alcorn, 1988). The sexual stage (telemorph) of *B. sorokiniana* is *Cochliobolus sativus* (Ito and Kurib.). The sexual stage is mainly known from laboratory cultures, but is also reported from the field in Zambia (Raemaekers, 1991). Another name used for the asexual stage in the literature is *Drechslera sorokiniana* ((Sacc.) Subram. and Jain). The conidia are curved to straight, fusiform, to broadly ellipsoidal and germinate by one germ tube from each end (bipolar germination). The size of the conidia is 40-120 x 17-28 µm and they have 3-12 distoseptates (Figure 2) (Sivanesan and Holliday, 1981). The conidia are able to germinate using endogenous energy reserves, but are stimulated by exogenous nutrients such as root exudates (Nilsson et al., 1993). Fungal infection of both leaves and roots comprises several phases: conidia germination, formation of appressoria, penetration, and colonisation (Yadav, 1981; Carlson et al., 1991). *Bipolaris sorokiniana* produces toxins which interact with host membranes resulting in cell death and leakage of metabolites (Marrè, 1980; Harborne, 1983). The phytotoxins induce both chlorosis and necrosis in plant tissue (Harborne, 1983). Carlson et al. (1991) found that the most active and abundant phytotoxin formed was prehelminthosporol ($C_{15}H_{24}O_2$). They found the toxin in conidia, hyphae and the surrounding culture medium.

Diseases and dispersal

Depending on the site of infection *B. sorokiniana* can cause different diseases like common root rot, spot blotch, seedling blight, foot rot and crown rot of wheat and barley (Lee, 1986). The diseases are increasingly important in barley in the cool climate of North-Western Europe (Jørgensen, 1974; Kurppa, 1984). Yield loss of up to 15% are reported (Piening, 1973; Olofsson, 1976; Stack, 1982; Kurppa, 1985; Forsberg, 2004). Earlier they were considered mainly as serious diseases of warmer cereal growing regions, chiefly North America, and parts of Australia and New Zealand (Sivanesan and Holliday, 1981). Severe yield losses, up to 100%, due to *B. sorokiniana* occur in Bangladesh, Bolivia, Brazil, Paraguay and Zambia (Mehta, 1997).

Also from South and Southeast Asia the diseases caused by *B. sorokiniana* are reported (Saari, 1997). Of the fungal pathogens of cereal crops in

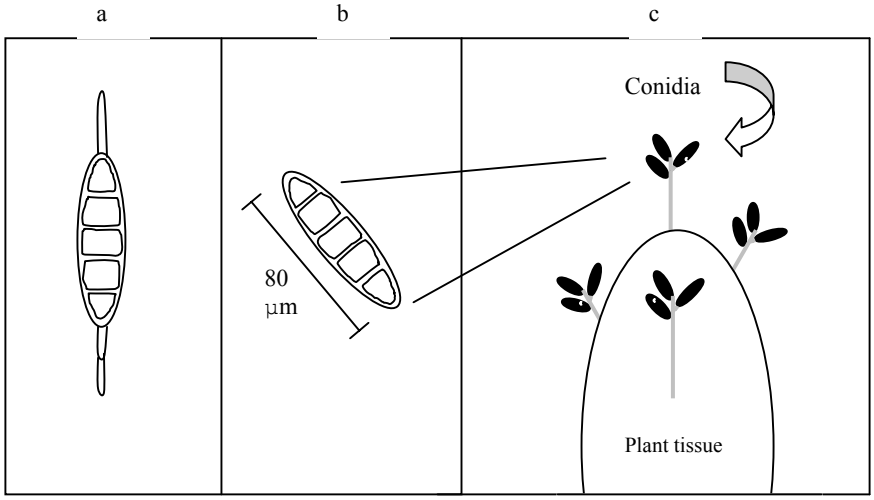

Figure 2. Bipolaris sorokiniana with; a) bipolar germination of the conidia, b) conidia with five distoseptates as seen on the microscope, c) black shiny conidia as seen on the binocular microscope.

Hungary, *Bipolaris* species have increased in importance (Bakonyi et al., 1998). Greenhouse experiments have shown that the pathogen can develop and induce the formation of leaf spots at as low temperatures as 6ºC (Dehne and Oerke, 1985). Symptom development, were intensified at temperatures higher than 20ºC, high relative humidities (>30%) and elevated light intensities (>3000 lx). However, incubation under temporary low light conditions accelerated senescence of leaves in a short time (Dehne and Oerke, 1985).

Bipolaris sorokiniana is seed-borne causing primary infection, soil-borne or disseminated by air currents that carry them as inert particles to various distances and cause secondary infections (Figure 3). In the soil the conidia are able to remain their infectivity capacity for at least 22 months (von Ammon, 1963) and may infect the following crop. Infection can take place through stomata on the hypocotyls, from where the fungus progress to the root, shoot and coleoptile (Sprague, 1950). Dark brown, lenticular spots of variable size form on the young leaf sheaths; post emergence death may occur. Roots show brown spotting or a more general necrosis. Conditions for the occurrence of secondary infection of barley are most favourable during the late growing season, when crops are nearly ripe and relative humidity is high for at least part of the day (Spurr and Kiesling, 1961). Air-borne secondary infection may result in necrotic spots on the leaf as well as infection in ripening seeds (Mead, 1942; Vendrig, 1956). The fungus may also spread symptomless on the plant and yield losses may even occur without severe disease symptoms (Kurppa, 1985).

Control measures

Bearing in mind the dispersal strategies of *B. sorokiniana* measures to control the diseases could be by I) avoiding the production of conidia, II) their ability to survive and infect in the soil, III) their ability to develop from seed-infections or IV) their ability to infect the green parts of the plant through the spread in the air. This could be done by a mixture of *B. sorokiniana* suppressing cultural practices. Kurppa (1985) found, while studying the soil-borne *B. sorokiniana*, that the inoculum density of the soil was of major importance, in terms of decreasing the growth of the barley plants, compared to fungal isolates or barley cultivars. The longer the time interval between susceptible hosts, the lower the ratings of common root rot (Ledingham, 1961). In crop rotations design to reduce the soil-inoculum density of *B. sorokiniana* low sporulation on oilseed rape and red clover indicates their suitability in the rotation (Duczek et al., 1996). Bailey et al. (1992) found that inoculum levels and isolation frequencies of *B. sorokiniana* in wheat was reduced by reduced tillage, wheres Reis (1990) found that no tillage favored inoculum production by common root rot because large numbers of conidia were produced on host residues left on the soil surface. There are significant differences in the reactions of barley cultivars to the fungus, but no complete resistance has been shown (Duczek, 1984; Kurppa, 1985). Considering chemical treatments, the postemergence herbicides 2,4-D, MCPP and dicamba are shown to increase *B. sorokiniana* disease severity on *Poa pratensis*, a host plant resistant to the herbicides in the studies (Hodges, 1978, 1984). Different herbicides also increase the sporulation of *B. sorokiniana* on *P. pratensis* leaf tissue of all ages (Hodges, 1992, 1994), which could influence inoculum potential of the soil and disease severity of a following barley crop.

Considering the seed-borne diseases, hot humid air treatments of the seeds are shown to reduce the yield loss due to *B. sorokiniana* (Forsberg, 2004), but are not commercialised. Seed treatments based on the bacteria *Pseudomonas chlororaphis* (Cedomon®) against the pathogens caused by *Drechslera* sp., is available but has uncertain effects against *B. sorokininana* (Bioagri, Sweden; Olvång, 2002). The seed-borne disease in conventional farming is usually controlled through the use of chemical seed treatment (Sivanesan and Holliday, 1981). The infections from soil-borne inoculum, including inoculum on plant debris are difficult to control by chemical seed treatments. The extent of pathogens may even increase as a result of the treatment of seeds with fungicides (Daamen, et al., 1988, 1989). It is possible that this increase is caused by the elimination of antagonistic organisms (Al-Hashimi and Perry, 1986). Knudsen et al. (1995) found that isolates of the fungi *Idriella bolleyi*, *Chaetomium* sp., and *Gliocladium roseum* inoculated on barley seeds acted as antagonists towards *B. sorokiniana*. In a six years field study, treatment of barley seed with *Idriella bolleyi* decreased the disease symptoms caused by *B. sorokiniana* by 16% and led to an average yield increase of 4% (Duczek, 1997). Furthermore, *I. bolleyi* inoculated on barley seeds are shown to cause systemic induced resistance on the plants to subsequent infection with *B. sorokiniana* (Liljeroth and Bryngelson, 2002). Also bacteria have shown to reduce infection frequency of *B. sorokiniana* (Zhang and Yuen, 1999).

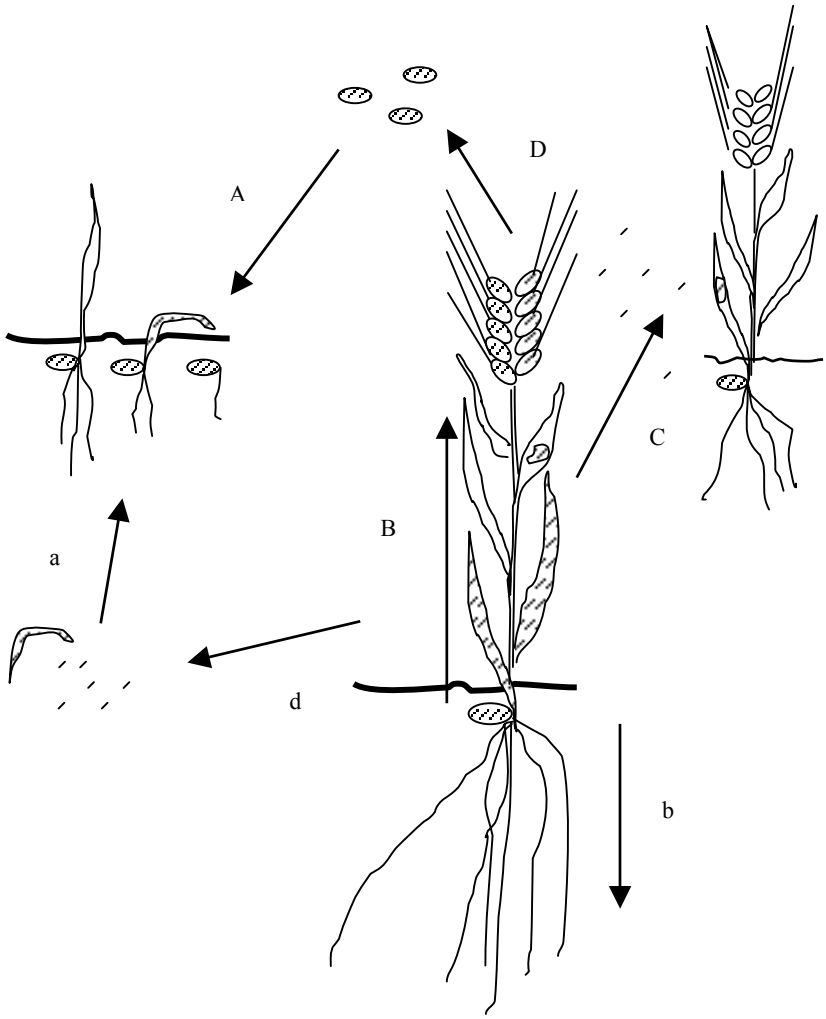

Figure 3. Disease cycle. Primary infection of a barley plant by overwintering *Bipolaris sorokiniana* in seed (A), or in the soil, either as conidia or as saprophytes on plant debris (a). The pathogen develop in the surviving plants with or without symptoms in the aerial plant parts (B) and to the roots (b). The conidia produced during the season may spread to different parts of other barley plants (C) or to weeds and cause a secondary infection. Finally, the pathogen survive to the next growing season in the seed (D) or in the soil (d).

In Australian fields, a decline in propagules of AM fungi during weed free fallow caused delayed root colonisation and poor growth of the next crop (Thompson, 1987). In proceeding studies Thompson and Wildermuth (1989) found that AM fungal colonisation of crop and pasture species was negatively correlated with root infection by *B. sorokiniana*. This indicates that AM fungi antagonise root infection by *B. sorokiniana.* However, they did not find a correlation between AM fungal colonisation and infection of stem bases with *B. sorokiniana*. Dehn and Dehne (1986) found a lower *C. sativus* (*B. sorokiniana*) infection of root tissue if the roots were already colonised by AM fungi.

AM fungi in disease control

The role of AM fungi in disease control have been studied in a number of plant pathogen – host species combinations. Borowicz (2001) showed that AM fungi reduced the detrimental effects of pathogens that extended beyond additive effects resulting from improved nutrition. This conclusion was made using a biometrically based examination (meta-analysis) of plant growth based on 22 papers considering the effects of AM fungi on plant-pathogen interactions. For effective control, inoculation of the AM fungus should generally take place prior to exposure to the pathogen, although there are a few exceptions known (Caron et al., 1986; St-Arnaud et al., 1997). Several AM fungal species have been found to control soil-borne pathogens, for example under greenhouse conditions *Glomus fasciculatum* and *Gigaspora margarita* are shown to decrease root rot diseases caused by *Fusarium oxysporum* f. sp. *asparagi* and *Helicobasidium mompa* in asparagus (*Asparagus officinalis* L.) (Matsubara et al., 2000; Matsubara et al., 2001) and *Glomus clarum* is shown to decrease root necroses due to *Rhizoctonia solani* in cowpea (*Vigna unguiculata* L.) (Abdel-Fattah and Shabana, 2002). In pasteurised soil AM fungi have shown to decrease the root damage caused by the root-rot fungus *Cylindrocladium spathiphylli* in bananas, although the pathogen decreased the intensity of AM fungal root colonisation (Declerck, et al., 2002). Newsham et al. (1994) found that AM fungi interact directly with root pathogens of the winter annual grass *Vulpia ciliata,* and improved fecundity by interfering with the negative effects of the pathogens. Results from the same study showed that the main benefit supplied by AM fungi to the plant was in protection from pathogen attack, not in phosphorus uptake. Considering foliar pathogens reports indicate that those are sometimes stimulated by AM symbioses (Meyer and Dehne, 1986; Shaul et al., 1999). However there are indications that foliar disease symptoms caused by a phytoplasma in tomato are reduced (Lingua et al., 2002). Studies have shown that some AM fungal colonisation also can increase disease incidence caused by soil-borne pathogens (Ross, 1972; Davis et al., 1978; Davis and Menge, 1980). Working with potato and *Rhizoctonia solani*, Mark and Cassells (1996) showed that different levels of control of the pathogen could sometimes be found with the same AM fungus on different cultivars of plants.

Mode of actions in biocontrol with bearing to B. sorokiniana *and AM fungi*

Competition for nutrients and space occur between pathogens and other micro-organisms (Wilson and Wisniewski, 1989; Wisniewski et al., 1989; Roberts, 1990; Mercier and Wilson, 1994). The importance of nutrients were also showed by

Droby et al. (1989), where an addition of exogenous nutrients to the interaction site resulted in decreased efficacy of the antagonist. With the knowledge of the nutrient flows in AM fungi it could be speculated that these fungi therefore are promising candidates for use in biocontrol. The extent to which the nutrient competition reduces infection may vary with the infection strategy of the pathogen involved. Fokkema (1971) found that the presence of pollen, highly stimulated the spore germination and the superficial growth of mycelium of the pathogen *Cochliobolus sativus* infection on rye leaves. This resulted in more penetration sites and an increase in necrotrophic leaf area. There was a positive correlation between the superficial mycelium density of *C. sativus* 2-3 days after inoculation and the necrotrophic leaf area. The presence of phyllosphere yeasts reduced the enhanced mycelium density and subsequent necrosis (Fokkema, 1973). Considering the competition for iron an advantage is the possible production of siderophores. Siderophores is a metabolic product which binds iron and facilitates its transport from the environment into the microbial cell. Fluorescent *Pseudomonas spp*. produces siderophores and are very efficient competitors for iron (Bakker et al., 1990), and competition for iron is one of the mechanisms responsible for soil suppressiveness to fusarium wilts (Scher and Baker, 1982; Lemanceau et al., 1988). There is some evidence that AM fungi may produce siderophores. The AM grass *Hilaria jamesii*, which showed greater iron uptake than a non-mycorrhizal control, tested positive for siderophores when bioassayed (Cress et al., 1986). Arbuscular mycorrhizal fungi are shown to suppress the plant diseases due to increased uptake of macro- and micronutrients or drought tolerance of the AM fungal plant. Alleviation of abiotic stress, such as decreased toxicity to salt and heavy metals by AM fungal colonised plants have shown to decrease disease in some cases (Hooker et al., 1994; Linderman, 1994; Karagiannidis et al., 2002). Altered root branching or root morphology due to AM fungal colonisation may also decrease the negative effect of plant pathogens (Norman et al., 1996; Fusconi et al., 1999). Between AM fungi and the pathogen there might also be a competition for energy derived from the photosynthesis of the host. This has been shown by Larsen and Bødker (2001) studying *Aphanomyces euteiches* in pea (*Pisum sativum*) the biomass of both the pathogen and the AM fungi decreased. The reduced AM fungal biomass can alter the micro-organisms surrounding the root (Hodge, 2000; Mansfeld-Giese et al., 2002), which might include bacteria antagonistic to plant pathogens (Andrade et al., 1997; Andrade et al., 1998; Citernesi et al., 1996).

Not only the rhizosphere, but also the mycorrhizosphere might favour the growth of micro-organisms antagonistic to plant pathogens (Filion et al., 1999; Norman and Hooker, 2000; Filion, et al., 2003). Soil micro-organisms influence AM fungal development and symbiosis establishment. Negative impacts include a reduction in spore germination and hyphal length in the extraradical stage, decreased root colonisation and a decline in the metabolic activity of the internal mycelium (Wyss et al., 1992; McAllister et al., 1995). There are also positive effects found; Azcon-Aguilar and Barea (1985) observed that colonisation of a plant by an AM fungus (*G. mosseae*) was stimulated by a strain of *Pseudomonas* sp. Gryndler and Vosatka (1996) found that *Pseudomonas putida* stimulated maize root colonisation by *Glomus fistulosum*, and that the dual inoculation had a

synergistic effect on plant growth. Similar results are observed in other studies (Azcon-Aguilar et al., 1986; Azcon, 1987; Linderman and Paulitz, 1990).

A nearly omnipresent feature of plant-pathogen interactions is host cell death. In some cases the cell death occur as rapid collapse of tissue, termed the hypersensitive response (HR). This response accompanies "incompatible interactions" and leads to disease resistance. The HR is programmed genetically in the plant and is a consequence of new host transcription and translation (Dixon et al., 1994; Godiard et al., 1994). A local HR is often associated with the onset of systemic acquired resistance (SAR; Chester, 1933; Enyedi et al., 1992; Ryals et al., 1994, 1996) in distal plant tissue. Some plant responses are very quickly, within hours, after the induction event (Zangerl and Berenbaum, 1995). However, some examples of SAR occur without this HR (Jakobek and Lindgren, 1993; van Loon et al., 1998). Furthermore, HR cell death is not always required to stop pathogen growth (Century et al., 1995; Hammond-Kosack et al., 1996). The SAR may also be triggered without plant cell death. On the contrary, necroses are equally a feature of disease symptoms during compatible interactions. The cells are often killed via the action of pathogen-derived toxins, which is one feature of *B. sorokiniana* (Marrè, 1980; Harborne, 1983). Necroses induced by compatible pathogens do induce SAR (Jenns and Kuc, 1977; Cohen and Kuc, 1981; Kuc, 1987). Plant control the ingress of potential fungal pathogens with increased activity of enzymes and accumulations of cell-wall proteins associated with defence. The enzymes that may accumulate is, for example, those which are involved in enhanced phenolic metabolism (Ryder et al., 1987), or the degrading of fungal cell walls (Hedrick et al. 1988; Edington et al., 1991). Enhanced accumulations of structural protein may increase the resistance of plant cell walls to enzymatic degradation by a potential pathogen (Cordier et al., 1998).

Plant defence-like responses to AM formation have been reported in several mycorrhizal systems during the initial stages of AM fungal colonisation (Spanu and Bonfante-Fasolo, 1988; Spanu et al., 1989). At later stages, the defence-like responses in AM fungal colonised roots dropped below levels in the controls with no added AM fungi. However, in other studies the accumulated plant-defence like responses remained at later stages (Harrison and Dixon, 1993, 1994; Blee and Anderson, 1996). Systemic suppression of AM fungi colonisation of barley roots already colonised by AM fungi has been indicated (Vierheilig et al., 2000).

Material and methods

The experimental set-ups used in the studies are summarised in Table 2, presenting which important factors considering barley - AM fungi - *B. sorokiniana* interactions that were included.

Indigenous AM fungal spores

To investigate the occurrence of AM fungi in Sweden, sampling sites were chosen on a broad range of arable fields in the country, in total 45 different sites (Paper I).

Table 2. *Experimental set-ups*

Factors studied	System	Design	Paper		
			I	II	III
Occurrence of AM fungi	Field sites	Field soil	√		
Transmission of *B. sorokiniana*	Non-sterile soil	Pots[a]		√	
Spot development on barley leafs	Gnotobiotic[b]	Bottles[c]			√
Growth of barley plants	Non-sterile soil	Pots[a]		√	
AM fungi root colonisation	Non-sterile soil	Pots[a]		√	
-"-	Gnotobiotic[b]	Bottles[c]			√
AM fungal spore germination	In vitro	Petri dishes			√
B. sorokiniana conidia germination	In vitro	Petri dishes			√

[a] In greenhouse; [b] Gnotobiotic = growth conditions in which all the living organisms are known; [c] In climate chamber.

The sites included both semi-natural grassland and ploughed fields. The localities were situated between 55.4˚and 65.4˚ North and between 13.2˚ and 21.2˚ West. The highest altitude was 707 meter above sea level. The samples were taken with a soil drill that was pushed down to 30 cm in the soil profiles. The soil cores were divided in two halves for comparison of the amount of AM fungal spores at different depths. All soil samples were analysed for their AM fungi spore content, by modification of the methods for wet sieving (Gerdemann and Nicolson, 1963) and centrifugation (Walker et al., 1982). The spore suspensions were then vacuum-filtered and the spores were counted on the filter papers under a compound microscope. The spores of a subset of the samples were mounted on microscope slides (Schenck and Péres, 1990) and identified to the level of genus or species. The samples chosen for determination of AM fungal diversity represented different agro-climatic zones and crops at the sampling time. All soils were also analysed for content of clay, phosphorus, nitrogen and carbon.

Greenhouse experiments

To get enough AM fungi for the greenhouse experiments the AM fungal populations from the field soils (Paper I) were multiplied in greenhouse using a mixture of plant species (Alexandrian clover, corn, leek, marigold, pea, sunflower, tomato, wheat and white clover), i.e. trap cultures. The mixture of plant species in the trap cultures did not include barley, to avoid multiplying possibly barley pathogens. Cores of field soil were placed onto trays containing a sand/silt mixture. Each tray represented a particular field. At maturity, plants were harvested and new seeds were sown. All experiments include controls with no added AM fungi. Information about the origin of the field soil used in the trap cultures are seen in Papers I and II. Each trap culture have a reference number, the same number are used in text and Tables.

A first screening survey was conducted with an aim to select for studies the most promising AM fungal populations with respect to their potential for reducing infection by *B. sorokiniana* in barley plants (Paper II). Soil inocula from eight different AM fungal trap cultures were chosen for the screening survey. The inocula were collected after the first generation of trap plants. Barley kernels with seed-borne *B. sorokiniana* were sawn in pots and soil inocula from the AM fungal

trap cultures were added. Since the AM fungal populations were added as soil inocula this made it possible to include all existing AM fungal species whether they had sporulated or not at the time for inocula collection in the trap cultures. At harvest the number of living plants in each pot was noted, as well as the height of the plants. The stem bases were cut and incubated in a moist chamber for analysis of *B. sorokiniana*.

In a second experiment with soil inocula from the AM fungal trap cultures in the greenhouse (Paper II), AM fungal trap cultures from two different origins were selected from the screening survey above. The inocula were collected from the trap cultures after the second generation of the plants. In addition a commercial inoculum was included (Vaminoc®, Becker Underwood, MicroBio) all three combined with three levels of *B. sorokiniana* seed infections (54%, 72%, 95%). Two controls were set up, lacking AM fungi; Control 1 (based on a substrate treated in the same way as the AM fungal trap cultures, but with no added AM fungi), Control 2 (a sand/silt mixture, with no added AM fungal inoculum). Barley kernels with seed-borne *B. sorokiniana* were sawn in pots. The plants were placed in the greenhouse. At harvest the number of living plants in each pot was noted, as well as the height of the plants. The stem bases, nodes and leaf spots were placed in a humid chamber for analysis of *B. sorokiniana*.

To avoid interference from other possible soil microorganisms an experiment was conducted with AM fungi added as spore mixtures (Paper II) from the AM fungal trap cultures. Arbuscular mycorrhiza fungi from one trap culture used in both previous experiments were chosen for the third greenhouse experiment. The spores were collected after the third generation of the trap plants. In addition AM fungi from eight other trap cultures with Swedish origins (Paper I) were chosen together with one commercial inoculum with *in vitro* cultured, surface sterile *G. intraradices* (see Paper II). The *B. sorokiniana* infected barley seeds were pre-germinated. The spores were added to the roots of the seedlings in small plastic trays to allow close contact between the AM fungi and the roots. The plastic trays with seedlings were transferred to pots and the plants were grown in greenhouse. At harvest root pieces, stem bases, stem and leaf parts at the base of each leaf and leaves were placed in a humid chamber for analysis of *B. sorokiniana*. For AM fungi colonisation studies, the roots were cold-stained (after Koske and Gemma, 1989; Grace and Stribley, 1991; Walker and Vestberg, 1994). This was found to be a more gentle method for the root rot affected roots compared to hot staining. The roots were spread onto Petri dishes and the AM fungi colonisation were observed under a binocular microscope and estimated as percentage of roots colonised. The amounts of necroses due to the pathogen were also recorded. Low levels of nutrients were maintained during the plant growth experiments.

In vitro studies

The mechanisms involved in the interactions between *B. sorokiniana* and AM fungi were studied in a series of experiments under sterile conditions (for details see Paper III). A technique was developed for studying the effect of AM fungi on disease development of pathogens on the host plant under gnotobiotic conditions.

The AM fungal species used in the experiments were *G. intraradices* and *G. proliferum*. The media used were 0.2% M medium (w/v. Bécard and Fortin, 1988), PDA (potato dextrose agar, Oxoid Ltd, 39 g per litre) and 1% water agar. In all experiments controls lacking the parameter (fungi, exudates filtrates) were included.

The direct interactions between *B. sorokiniana* and AM fungi where studied by co-culturing on the same medium. The effect of possible volatile compounds produced by either *B. sorokiniana* or *G. intraradices* was studied by culturing the two organisms on one Petri dish devided from each other by a plastic slide. Effect of exudate filtrates of *B. sorokiniana* on AM fungi were studied. The exudate filtrates were spread on top of M medium before the AM fungal spores were added. Extract of *G. intraradices* hyphae grown on transgenic carrot roots (separated from the roots with a plastic slide) was also obtained and the effect on conidia germination of *B. sorokiniana* was studied. The effects were observed by colony-diameter of *B. sorokininana*, spore- or conidia germinations and hyphal growth of germinated AM fungal spores.

Since the AM fungi are obligate symbionts it has not been possible to grow these fungi *in vitro* until relatively resently. Mosse and Hepper (1975) reported the use of root organ culture to obtain typical infections with *Glomus mosseae in vitro* and Mugnier and Mosse (1987) have developed a method using Ri T-DNA transformed roots. The methods were developed further by Bécard and Fortin (1988). Since then several interaction studies have been conducted *in vitro* between AM fungi and the transgenic roots. In present work, a method was developed for studying the effect of an established AM fungi colonisation in non-transgenic barley roots on the disease development of *B. sorokiniana* infected leaves *in vitro* (for details see Paper III). Pieces of transgenic carrot roots colonised with *G. intraradices* were inoculated in bottles with M medium. The AM fungi were allowed to develop a network of hyphae in the medium for six months, since a living hyphal network is important in initiating rapid colonisation in seedlings (Read, et al., 1985; Read, 1992), before the seedlings were inserted. The result was a rapid colonisation of the barley roots of AM fungi. Seeds of barley were surface sterilised (after Åström, 1990) and pre-germinated. The seedlings were placed in one bottle each and covered with a layer of Vermiculite (Askania, Göteborg, Sweden). A figure describing the experimental set-up is seen in Paper III; Figure 1. The bottles were placed in a growing chamber, after one week plugs of *B. sorokiniana* grown on water agar were inoculated on the barley leaves. When the lesions (necroses developed as a symptom of the disease initiated by *B. sorokiniana*) started to develope their lengths were measured each day. The roots were cold-stained (after Koske and Gemma, 1989; Grace and Stribley, 1991; Walker and Vestberg, 1994) and the AM fungal colonisation was studied under binocular microscope.

Results and Discussion

The plant pathogenic fungus *B. sorokiniana* has the capacity to infect the host directly on the leaf, while air-borne, on the roots, while soil-borne or through the seed, while seed-borne. It is therefore important to consider the diverse infection strategies if aiming to develop tools for biocontrol. While earlier workers have shown that AM fungi are able to suppress the *B. sorokiniana* in the roots, there was a lack of information concerning the interaction in the aerial parts of the plants. Reports on foliar diseases have indicated that the pathogens are enhanced by AM fungi (Whipps, 2004). Is this the case also for the development of *B. sorokiniana* from seed infection to the aerial plant parts? It could also be suggested that there is a difference between isolates of AM fungi in their possible ability to suppress the pathogenic fungus in aerial plant parts. Having found out that several multiplied field populations of AM fungi suppress the *B. sorokiniana* in stems and leaves, even through the pathogen had an advantage in that it was seed-borne and having seen that the pathogen was suppressed although the AM fungal colonisation was low I wondered how do these two fungi interact within the soil? Being such a successful pathogen, *B. sorokiniana* might have a competition advantage in the soil against the commonly occuring AM fungi. Lastly, I wondered how does the AM fungi affect the air-borne *B. sorokiniana* infecting the host leaves and how is it possible to study this without any influence of other organisms?

AM fungi occurrence

As it was hypothesised, AM fungi differs in characters depending on their origin; and since there was only scarce data on AM fungi in Sweden (Mårtensson and Carlgren, 1994; Eriksson, 2001; Hedlund, 2002) a first step was to make a survey of AM fungi under various prevailing climatic/cultivation conditions. The idea was to cover the broad spectrum of commonly occurring agroecosystems in Sweden. Therefore, sampling sites were chosen in different agro-climatic zones, based on both climatic and soil properties (Carling and Joner, 1998). In each zone samples were taken from both ploughed and unploughed arable fields, i.e. semi-natural grasslands. The ploughed fields chosen were cultivated using agricultural practices common for each area.

Arbuscular mycorrhizal fungi were found to be present at all sampling sites in this study. This shows that the AM fungi and its symbiosis with plants are widely spread in agricultural fields in Sweden. Arbuscular mycorrhizal fungi have also been found in other Northern areas, although not to the same extent as reported in Paper I. Vestberg (1995) found AM fungi spores in half of the 266 indigenous soil samples taken from different parts of Finland (61-68°North). However, the presence of AM fungi were detected after multiplication on trap plants, thus there might have been AM fungi present in a higher proportion of the indigenous samples, although they did not form spores in the trap cultures. At even higher latitudes (74-80°North) in the Arctic, AM fungal spores have been found in the indigenous soil of 9 out of 13 collected sites, at densities between 1-3 spores per g

soil (Dalpé and Aiken, 1998). They took the soil samples from the rhizosphere of *Festuca* species growing in the tundra. At the sampling location in Sweden with the highest latitude (65.4°North), Hindersön situated on an island in the Baltic Sea, the spore densities was as high as 21 spores per g dry soil (Paper 1; Table 1-2). Overall the spore densities found ranged between 3-44 spore per g dry weight of soil in this study. The lowest spore density was found in a cereal monoculture, and the highest spore density in a semi-natural grassland. There were significantly more AM fungal spores in the upper half than in the lower half of the top 30 cm of the soil profiles. This relationship was not affected by ploughing. Other studies also show a decline in spore densities down the soil profiles (Jakobsen and Nielsen, 1983; Abbot and Robson, 1991). Multivariate statistics in terms of Principal Component Analysis did not show any groupings of the spore densities according to physical analysis, crop or agroclimatic zones of the sampling sites.

Diversity and symbiotic effectiveness

Between three and seven AM fungal spore types were found at the eight sampling localities in which spores were identified (Paper I). Most species belonged to *Glomus* spp., but species within *Scutellospora* were also found. The two samples with highest number of spore types originated from the two semi-natural grasslands, with high plant diversities, no ploughing and no addition of fertilisers. The six samples with lower number of spore types originated from more intensively managed ploughed fields, with low plant diversities. However, there may probably be more AM fungal species present, since all species might not have sporulated at the sampling time (Miller et al., 1985). For example, *Glomus mosseae* was not found in the indigenous soil samples, although this is a common species found in temperate climate (Vestberg, 1995). However, spores of *Glomus mosseae* type (Figure 4) were found in one of the AM fungal trap cultures of indigenous soils (Paper I, Table 2; trap culture no 43).

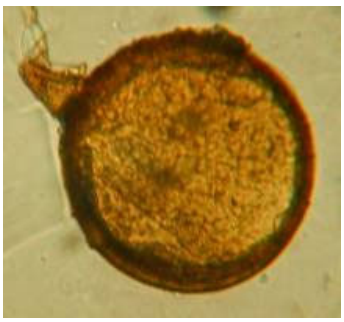

Figure 4. Arbuscular mycorrhizal fungal spores in close resemblance with *Glomus mosseae.*

Burrows and Pfleger (2002) also found more AM fungal species at higher plant diversity. Jansa et al. (2002) found that the community structure of AM fungi in the field soil was affected by tillage treatment, but there were no difference in AM fungal diversity. In an Indonesian study soil disturbance reduced the density of spores, species richness and the lengths of extra-radical mycelium of AM fungi

(Boddington and Dodd, 2000). Also in temperate zones the hyphal density of AM fungi is shown to be reduced by ploughing (Kabir et al., 1998). Soil disturbance clearly affect the AM fungi. By ploughing the soil almost every year, the AM fungal species that dominate is probable adapted to disturbance (Oehl et al., 2003). This adaptation may in turn affect the quality of the AM fungal communities. Consequently, it might be possible to improve the mutualistic value (symbiotic effectiveness) of the AM fungal communities by adjusting the agricultural practises. Boddington and Dodd (2000 a, b) showed that AM fungi from different genera respond differently not only to disturbance but also to addition of phosphate fertiliser. As noted by Janos (1993) symbiotic effectiveness depends on the interactions between "mycorrhizal plant × mycorrhizal fungus × soil characteristics".

Both the plant and the soil characteristics are possible to adjust by agricultural practices and thereby the effectiveness of the indigenous AM fungi. Plenchette (1983) defined the mycorrhizal dependency of a plant based on the relationship between dry mass of the plants inoculated with a mycorrhizal fungus and the dry mass of uninoculated plants. Fungal isolates within one species vary in mycorrhizal effectiveness. When tested on a single host plant species, different mycorrhizal fungus isolates can increase, decrease, or have little effect on plant growth (Burgess et al., 1994; Dosskey et al., 1990; Miller et al., 1985; Molina, 1979). Van der Heijden and Kuyper (2001) in addition to plant biomass, included N- and P-contents of the plant to describe symbiotic effectiveness. While working with plant pathogens in small grain it would be possible to define the symbiotic effectiveness of AM fungi by the grain yield (both quantitatively and qualitatively) and the inhibition of the pathogen development (not only affecting the yield, but also the inoculum production of the pathogen). Van der Heijden and Kuyper (2001) found that "plant origin" and "plant origin × soil type" had a large interaction on the symbiotic effectiveness both for AM fungi and ectomycorrhizal fungi. In their study it can be noted that ectomycorrhiza fungal origin had only a minor effect on symbiotic effectiveness. However, since their study of the fungal origin was only performed with ectomycorrhizal fungi, van der Heijden and Kuyper (2001) proposed that this was due to the fact that spores of ectomycorrhizal fungi spread more efficiently than seeds. While considering the AM fungi this relationship is the opposite, the AM fungi with their spores solely produced in the soil or roots would spread much less efficiently than most plant seeds.

AM fungi suppressiveness of *B. sorokiniana*

The amount of AM fungal spores or their diversity does not tell to which extent the roots are colonised. More important, it does not tell what function the AM fungi have in the agroecosystem. One possible feature for the AM fungi is to reduce plant diseases. Following the extensive field survey the hypotheses was that the ability of AM fungi to suppress plant pathogens differed with the origin of the mycorrhizal fungi. By studying AM fungal populations from, for many years commonly cultivated, fields it is possible to identify AM fungi that can tolerate the impact of agriculture. Arbuscular mycorrhizal fungi collected from arable fields

are therefore of value, both for the possibility to define agricultural practises stimulating symbiotic efficient AM fungi and for the option to use the AM fungi for disease suppression in practical farming.

In Paper II, AM fungi originating from fields of different agro climatic zones and crops, investigated in Paper I, were selected for a screening, considering their ability to interact with *B. sorokiniana*. Results of the survey showed that all, but two, AM fungal trap culture added as soil inocula resulted in a lower development of *B. sorokiniana* from the seed to the stem bases compared to the development of the pathogen in the plants with no added soil inocula from AM fungal trap cultures. One possible reason for this seems to be the elimination of AM fungi in sterilised soil.

Another interesting observation is the difference in inhibition between soil inocula from trap cultures of different origin. In the screening, AM fungi originating from a semi-natural grassland (Paper I; Table 2; trap culture no 29) indicated a beneficial effect on the germination of the *B. sorokiniana*-infected seeds and the survival of the barley plants. This trap culture originated from the indigenous soil with the highest number of different AM fungal spore types (Paper I). Among those AM fungal species there might have been some with opportunistic ability to colonise the first roots emerging from the seeds or at an early stage in other ways favouring the survival and growth of the barley plant. In semi-natural grasslands there is a dense layer of roots of several species of perennial grasses and herbs, which always might be colonised by AM fungi. However, every now and then there will be gaps in the plant cover, which will give new opportunities for seeds and AM fungi. Under such circumstances, a quick colonisation by AM fungi will be an ecological advantage. Based on this assumption, trap culture inocula originating from this semi-natural grassland were therefore selected for the second study.

The soil inoculum from the trap culture that gave rise to the highest percentage of healthy stem bases at harvest were the most disease suppressive and was also selected for the second experiment (Paper II; Table 2; trap culture no 41). This trap culture could possibly contain AM fungi to inhibit the development of *B. sorokiniana* to the stem bases. This trap culture inoculum originated from a farm that had been organically managed for several years, thus no chemical seed treatments were used inhibiting possible *B. sorokiniana* antagonistic AM fungi. The original soil was cultivated with barley with undersown ley at the sampling time, which might mean presence of multiplied AM fungi with a preference for barley. In addition, the undersown ley increase the plant diversity and thereby may promote a higher AM fungal diversity. However, the proportion healthy stem bases were also relatively high for the barley plants growing in pots inoculated with trap cultures originating from a barley field in the northern part of the country (Paper II; Table 2; soil number 6) as well as those originating from a field with ley in the southern part of the country (Paper II; Table 2; trap culture no 43).

In the successive study soil inocula from a trap culture originating from the semi-natural grassland with trap culture no 29 (Paper II; Table 1) and the barley field with trap culture no 41 (Paper II; Table 1) gave similar results as in the preceeding screening; trap culture inoculum originating from the semi-natural

grassland resulted in more living plants and taller plants at harvest, while trap culture inoculum originating from the organically managed barley field resulted in a tendency for lower amounts of *B. sorokiniana* being detected on the stem bases (Paper II; Table 4). The trap culture inocula of native origins from Sweden were more efficient in inhibiting the development of *B. sorokiniana*, compared to the AM fungal commercial inoculum (Vaminoc®) included in the study (Table 5). This indicate that although the AM fungi might have general benefits for the crop production AM fungi from different origins differ in their abilities to suppress specific pathogens.

It should however be remembered that also the commercial inoculum inhibited the development of *B. sorokiniana* upwards the barley stems (Paper II; Table 5). A speculation is also that the AM fungi from the semi-natural grassland might not be adapted to circumstances in more intensively cultivated fields, including ploughing. Therefore, the AM fungi originating from semi-natural grassland were not included in the proceeding experiment. For a third greenhouse experiment, using spore inocula, the AM fungi originating from the organically managed barley field (Paper II; Table 1; reference number 41) were used, in addition to AM fungi from other ploughed fields.

In the soil inocula from the trap cultures, there are probably other micro organisms than AM fungi multiplied as well, which could have an influence on the pathogen and/or the plant (Alström, 1987; Åström, 1990; Knudsen et al., 1997). By using AM fungal spore mixture as inocula in a third experiment such microorganisms were avoided. Possible differences between the substrates were also avoided, which could have an influence of the result (e.g. substate of Vaminoc® and trap cultures respectively). The inocula thus contained the AM fungi that had sporulated at the time for inocula collection and had also managed to survive the storage time of six months. For the option to inoculate AM fungi into arable fields in the practical farming the ability of the AM fungi to remain viable during storage is of great value, although there is a potential for optimising the storage method. The spores were surface washed to reduce bacteria. The spore inocula thus obtained consisted of AM fungi and possible mycorrhiza associated bacteria (Garbaye, 1994). This is the same situation as in the arable fields, where the AM fungi is living in an environment surrounded by other microorganisms, thus the spores are never sterile on the surface *in vivo*. In present experiment with AM fungi spore inocula, the barley plants treated with AM fungi from either of the origin resulted in lower detection of *B. sorokiniana* on leaf bases, leaves and stem bases. Also the commercial inoculum with surface sterilised *Glomus intraradices* spores had a lower incidence of *B. sorokiniana* than the control, which show that AM fungi with no initial bacteria on the surface have an suppressive effect against *B. sorokiniana*. Multivariate statistics in terms of Principal Component Analysis did not show any groupings of the suppressiveness of *B. sorokiniana* in relation to physical analysis, crop or agroclimatic zones of the sites from where the trap cultures originated (Paper I). In the screening survey in Paper II there was a slight tendency for increased suppression of the pathogen with decreasing amount of easily available phosphorus in the indigenous soil from where the trap culture originated, but this was not statistically confirmed. However, the relationship

between the function of the AM fungal isolates and parameters describing the collection site is important for the understanding of the AM systems.

Presented results may indicate that the AM fungi decrease the root-necroses caused by *B. sorokiniana* (Paper II), since the roots of the plants lacking AM fungi had the highest proportion of necroses. This is in accordance with the result of Dehn and Dehne (1986) who found a lower *Cochliobolus sativus* (*B. sorokiniana*) infection of root tissue if the roots were already colonised by AM fungi, in this case *Glomus etunicatum*. They proposed that the mechanism mediating the mycorrhiza-Common root rot interactions was correlated to a general change of host plant physiology induced by the establishment of the AM symbiosis. All three isolates of one AM fungal species tested were able to reduce disease intensity on the roots (Dehn and Dehne, 1986). Furthermore, disease intensity could be reduced by AM fungi in all ten varieties of wheat and barley tested, but the degree of resistance varied with the genotype of host and pathogen (three *C. sativus* isolates were included). However, the degree of AM fungi colonisation of barley root was not correlated to their inhibition of common root rot (Dehn and Dehne, 1986).

In the present study the development of *B. sorokiniana* in stem bases, leaf bases, and leaves were inhibited although the AM fungi root colonisation was low (Paper II). This shows that AM fungi are able to suppress the *B. sorokiniana* development in barley plants, not only in the roots as shown by Dehn and Dehne (1986), but also in the above ground parts of the plants were the AM fungi is not present. Importantly, the pathogen was suppressed although the non-AM fungal plants was taller, which show that non-P-mediated mechanisms may be involved. This may indicate SAR and in that case seem to be initiated also with a low degree of AM fungal colonisation, although the mechanism mediating the mycorrhiza-disease interactions needs further investigation. The plant inoculated with AM fungal spores originating from the barley seed with undersown ley (Paper II; Table 1; trap culture no 41) had a three times lower risk of having a leaf base or leaf infected with *B. sorokiniana* (Paper II, Table 6) compared to the control, lacking AM fungi. Almost all other plants inoculated with AM fungal spores from other origins had an even lower risk of having a leaf base or leaf spot infected with *B. sorokiniana*. The AM fungal spores giving rise to the healthiest plants, with less than ten times lower risk of having a leaf base or leaf infected with *B. sorokiniana* (Paper II, Table 6) originated from fields with winter-wheat and barley respectively (Paper II, Table 1, trap culture no 23 and 33). In an Australian study AM fungal colonisation of crop and pasture species was negatively correlated with root infection by *B. sorokiniana* (Thompson and Wildermuth, 1989). They proposed that this indicates that AM fungi antagonise root infection by *B. sorokiniana.* It seems like the pathogen is locally inhibited by the AM fungus in tissues already colonised by the AM fungus, but the pathogen are able to infect AM fungi free tissues. However, the presence of AM fungi also seem to induce a change of host plant physiology independent of the degree of colonisation (Dehn and Dehne, 1986; Paper II, Paper III). This might explain why Thompson and Wildermuth (1989) did not find a correlation between degree of AM fungal colonisation and infection of stem bases with *B. sorokiniana*.

An attempt to explain observed responses by AM fungi towards *B. sorokiniana* in the plant is by means of SAR, but can also be due to an altered nutrient status of the plant. However, an improved nutrient status due to AM fungal colonisation is often shown to be correlated to an increase in foliar diseases (Whipps, 2004). To be able to study the development of the necroses on the leaf of the actual host species, with only the AM fungi and the pathogen present an *in vitro* method was developed. For *in vitro* studies, of the AM fungal effect in the plant to inoculation of a pathogen, so far transgenic carrot roots have been used, which are normally resistant to the pathogen examined (Benhamou et al., 1994). The developed method makes it possible to analyse possible biochemical differences between mycorrhizal and nonmycorrhizal host plants, challenged by a pathogen. The leaf spots caused by *B. sorokiniana* were shorter on the plants inoculated with AM fungi, compared to the control plants, lacking AM fungi at all times (Paper III, Figure 2). The M-medium was chosen since this is a common growth medium for AM fungal cultures. By using a medium with less amount of carbon it would be possible to further develop this technique for studying the effect of *B. sorokiniana* or other pathogens inoculated in the roots. With M-medium the *B. sorokiniana* seem to prefer the medium and not the root. It would also be possible to use different levels of, for example, phosphorus in the media. A further development of *in vitro* techniques for studying the effect of AM fungi on disease development in different host plants or the mechanisms involved would be to grow AM fungal colonised plants in meristem cultures (Morel and Martin, 1952; Conger, 1981) or in embryo cultures (Hännig, 1904; Lange, 1969; Yeung et al., 1981). Meristem and embryo cultures are used for *in vitro* cultivation of plant pathogen free material. Although these techniques are probably more time consuming, than surface sterilising of seeds, and the survival of the plant material might be reduced in the initial stage, this would probably give rise to less contaminations of unwanted organisms in the actual experiments.

Competition

Evolutionary, plants have evolved with both the AM fungi and the pathogens present. Consequently, since *B. sorokiniana* and AM fungi live in the same habitats, the soil and the root, these organisms also evolved together and probably developed defence strategies towards each other. One strategy by the AM fungi seem to be the induction of SAR restricting the development of *B. sorokiniana*, although more research is needed to explore the biochemical changes and to exclude the possible influence of an altered nutrient status. Other strategies might develop in the soil, for example at the pre-infection/colonisation stage, when AM fungi presumably do not have the ability to gain more energy in contrast to *B. sorokiniana* with its ability to live saprophytically. Aiming to develop tools for biocontrol, it is desirable to identify the interactions between the pathogen and the potential biocontrol agent. The observation from this study that there was a low AM fungal colonisation in the roots of the barley plants naturally infected with seed-borne *B. sorokiniana* (Paper II) led to the suspicion that *B. sorokiniana* might as well inhibit the AM fungi. Therefore, a series of *in vitro* studies were conducted. In addition, the possible direct inhibition of *B. sorokiniana* conidia germination by exudate filtrates of AM fungal extraradical mycelium were

examined (Paper III). Roots produce a huge array of organic chemicals of which are released to the surrounding soil (Rovira, 1969; Whitfield et al., 1981; Curl and Truelove, 1986). The compounds that are released by roots were classified by Rovira and Daveys (1974) according to their mobility in soil; 1) diffusible-water soluble, 2) diffusible-volatile and 3) non-diffusible compounds. The efficacy of volatile compounds as messengers in soil is well documented (Stotzky and Schenck, 1976). The germination and hyphal growth of AM fungal spores are also influenced by different compounds released by soil micro-organisms (Mc Allister et al., 1996; Paper III). Paper III showed that AM fungal spore germination are reduced by the presence both of *B. sorokiniana* growing on the same medium, or by its exudate filtrates or volatile compounds released by the plant pathogen while growing in nutrient rich medium. However, the possible volatile compounds did not affect AM spore germination when the plant pathogen was growing in nutrient deficient medium.

In practical farming this might mean that less nutrient near the germinating seed promote the AM fungal spore germination in the presence of soil-borne *B. sorokiniana*. The presence of exudate filtrates of *B. sorokiniana* inhibited the *Glomus intraradices* spore germination day 4-8. Later there were no inhibition, which might be due to the fact that the exudate had diffused down in the media. Different AM fungal species, or even different isolates of AM fungal species might however react differently towards *B. sorokiniana* and the reaction in laboratory might not be the same as in the field. However Paper III shows that exudate filtrates of *B. sorokiniana* inhibit not only *G. intraradices*, but also *G. proliferum* and this inhibition proceded at least until day 19. For statistical reasons, the hyphal growth of the germinated spores were divided in two categories, those that only grow a short distance and those that went on growing and branching. The statistical analyses thus did not show any difference in hyphal growth for the *B. sorokiniana* treated AM fungal spores and the control (which was not treated with *B. sorokiniana*) in any of the experiments. However, there might still have been differences in hyphal growth in a smaller scale (length of hyphae at different time intervals). For further comparisons of the hyphal growth a higher number of germinated AM fungal spores have to be analysed.

The conidia germination of *B. sorokiniana* does not seem to be affected by exudate filtrates of AM fungi to any great extent (Paper III; Table 4). However, the direct interaction between *B. sorokiniana* and a developed AM fungal hyphal network connected to living roots need to be examined as well as the ability of AM fungi, with ability to suppress *B. sorokiniana*, to suppress other pathogens. Development of methods for favouring the germination and establishment of AM fungi on the barley seedlings in the field to prevent infection by air-, seed- or soil-borne infections and/or transmission of pathogens is crucial. The pathogens provide all the signals that the plant has evolved to react to in terms of defences. However, the pathogen cause some level of economic loss to the crop. Arbuscular mycorrhizal fungi also evolved with the plant. Studies show that AM fungi induce defence mechanisms in the plant towards certain pathogens under some growing conditions (Cordier, et al., 1998; Paper II; Paper III). In contrast to the pathogen the AM fungi often not even cause trivial or unmeasurable levels of damage to the

crop, but actually also give several other benefits to the plant, like increase the phosphorus uptake and the resistance towards *B. sorokiniana*.

By identifying circumstances when the AM fungi best protect the crop against pathogens, tools will be available to exploit the AM fungi. There are several possibilities by using the AM fungi to reduce the loss in quality and quantity of the yield due to the pathogens caused by *B. sorokininan*. One option might be to introduce an alien AM fungi, which have been selected in screenings to have a high level of suppression ability of the pathogen, to the field. Due to the obligate biotrophic nature of the AM fungi they are relatively costly to multiply. In addition, it might be difficult to predict the activity of the specific AM fungi introduced, since soil biological parameters vary substantially. A better option might be to elaborate the cultivation practises to promote the mutualistic value of the AM fungal communities already existing. In addition, this could be combined with the addition of saprophytic bacteria or fungi acting by other modes of action against the pathogen than the AM fungi. This might give synergistic effects.

Conclusions

With this work I have been able to conclude that;

- arbuscular mycorrhizal fungi are present in a wide range of arable fields in Sweden, at the 45 sampling sites the AM fungal spore densities varied from 3 up to 44 spores per gram air dried soil,

- arbuscular mycorrhiza fungal trap cultures, pure *G. intraradices* and unsterilised spore-mixtures of arbuscular mycorrhizal fungi are able to suppress the development of seed-borne *B. sorokiniana* in barley. The degree of suppression of the development of *B. sorokiniana* varies with the origin of arbuscular mycorrhiza fungal trap cultures and unsterilised spore-mixtures of arbuscular mycorrhizal fungi,

- *in vitro* studies showed that *Bipolaris sorokiniana* decrease spore germination of AM fungal species,

- *in vitro* studies indicate that presence of AM fungi decrease the lesion development of the leaf due to inoculation of *B. sorokiniana*,

- by using the developed *in vitro* host plant method it will be possible to study the impact of AM fungi on the development of plant foliar diseases.

Thus, it is a clear potential for using AM fungi in crop production, not only to promote crop growth in general, but also specifically to suppress diseases caused by *B. sorokiniana*.

Abbreviations

AM fungi	Arbuscular mycorrhizal fungi
HR	Hypersensitive response
SAR	Systemic Aquired Resistance

Glossary of useful terms

Antagonism	the inhibitory action of one species on another
Arbuscule	complex branched treelike, hyphal systems within the cell of the plant root
Biotroph	an organism that can live and multiply on another living organism
Chlorosis	yellowing of normally green tissue due to chlorophyll destruction or failure of chlorophyll formation
Conidia	non-motile, asexual spores
Cotyledon	the first leaf or leaves of a seed plant, found in the embryo, and which may form the first photosynthetic leaves or may remain below ground
Distoseptates	individual cells each surrounded by a sac-like wall distinct from the outer wall
Fungal pegs	penetration of plant epidermal cells by individual hyphal "pegs" in monotropoid mycorrhiza
Fungicide	a compound toxic to fungi
Gnotobiotics	the study of organisms or species when other organisms or species are absent
Herbicide	a compound toxic to plants
Hypha	tubular filament that is the structural growth unit of filamentous fungi
Hypocotyls	that portion of stem below cotyledons in plant embryo, which eventually bears the roots
Mycelium	network of hyphae, the characteristic vegetative phase of many fungi
Mycorrhiza	the symbiotic association between a fungi and a plant
Mycorrhizosphere	the soil influenced by the mycorrhizal roots and mycelia
Necrosis	death of cells or tissues
Obligate	limited to one mode of life or action
Opportunistic	species specialised to exploit newly opened habitat
Peleton	hyphal coils formed in cortical cells in orchidaceous mycorrhiza
Phylum	a taxonomic rank between kingdom and class; a division
Rhizosphere	the soil influenced by roots
Saprotroph	organism that feeds on dead organic matter

Siderophore	a metabolic product of a fungus (or other organism) which binds iron and facilitates its transport from the environment into the microbial cell (from the Greek meaning “iron carrier”)
Specificity	being limited to a species
Vesicles	lipid rich storage organ

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